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Höffle, Hannes; van Damme, Cindy J. G.; Fox, Clive J.; Lelièvre, Stéphanie; Loots, Christophe ; Nash, Richard D.M.; Vaz, Sandrine ; Wright, Peter J.; Munk, Peter

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1 **Running title:** Fish egg distribution in the North Sea

2

3 **Linking spawning ground extent to environmental factors - patterns and**
4 **dispersal during the egg phase of four North Sea fishes.**

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6 *HANNES HÖFFLE¹*, CINDY J. G. VAN DAMME², CLIVE FOX³, STÉPHANIE LELIÈVRE⁴,*
7 *CHRISTOPHE LOOTS⁴, RICHARD D. M. NASH⁵, SANDRINE VAZ⁶, PETER J. WRIGHT⁷*
8 *AND PETER MUNK¹*

9

10 ¹*DTU Aqua, National Institute of Aquatic Resources, Technical University of Denmark,*
11 *Kavalergården 6, DK-2920 Charlottenlund, DENMARK*

12 ²*IMARES, Institute for Marine Resources and Ecosystem Studies, Haringkade 1, 1976 CP,*
13 *IJmuiden, The Netherlands*

14 ³*Scottish Association for Marine Science, Scottish Marine Institute, Oban, PA37 1QA, UK*

15 ⁴*IFREMER, Laboratoire Ressources Halieutiques, 150 quai Gambetta, BP699, F-62321,*
16 *Boulogne sur Mer, France*

17 ⁵*Institute of Marine Research and Hjort Centre for Marine Ecosystem Dynamics, PO Box*
18 *1870 Nordnes, 5817 Bergen, Norway.*

19 ⁶*IFREMER, UMR MARBEC, Avenue Jean Monnet, CS 30171, F- 34203, Sète Cedex, France*

20 ⁷*Marine Scotland Science, Marine Laboratory, 375 Victoria Road, Aberdeen, Scotland, AB11*
21 *9DB*

22

23 **Correspondence. Queen's University Belfast, School of Biological Sciences, Medical*
24 *Biology Centre, 97 Lisburn Road, Belfast BT9 7BL, Northern Ireland, Tel. +44 (0)28 9024*
25 *2464, h.hoffle@qub.ac.uk*

Abstract

Previous studies have shown that four commercially important demersal species, namely cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) and plaice (*Pleuronectes platessa*) spawn in distinct areas across the North Sea. Based on two comprehensive ichthyoplankton surveys in 2004 and 2009, the present study uses Generalized Additive Mixed Models (GAMMs) to delimit these spawning grounds using the distribution of recently spawned eggs, investigates their relationship to specific environmental conditions and examines egg dispersal during their development. Results indicate that presence/absence of early stage eggs is more related to temporal and topographic variables, while egg densities are closely linked with hydrography. Egg distribution patterns were relatively consistent during development and only changed near hatching. Compared to historic observations, the location of the spawning grounds appeared stable on the broad scale but centres of egg abundance varied between the surveyed years. Potential effects of long-term climate change and anthropogenic short-term disturbances, such as seismic surveys, on fish reproduction are discussed, pointing out the demand for multi-species studies on these issues.

Keywords: Spawning distribution, dispersal, seismic surveys, climate change, demersal fish

47 **Introduction**

48 Annually visited spawning grounds are a common feature in the life cycle of many fish
49 populations (Daan et al. 1981; Heath et al. 1994), and have been demonstrated for a number
50 of commercially important fish species in the North Sea (e.g. Brander 1994; González-Irusta
51 and Wright 2016a; 2016b). Such stability in reproductive strategy is thought to have evolved
52 to ensure that, during the average lifetime enough offspring are placed into suitable
53 environments to ensure the population's survival. Suitable conditions for survival may be
54 found in the vicinity of the spawning ground or in nurseries with good connectivity to the
55 spawning grounds. Bakun (1996) coined the term 'ocean triads' for areas where zooplankton
56 is plentiful due to enrichment from nutrients, and where fish offspring are retained in a given
57 water mass. In the North Sea, such conditions could be found at tidal and salinity fronts
58 (Simpson et al. 1993). For fish spawning in late winter and spring salinity fronts may be more
59 important (Munk et al. 2002; Munk et al. 2009) as increased freshwater runoff during fall and
60 winter widens the region of freshwater influence (ROFI), particularly in the southern North
61 Sea (Simpson et al. 1991). Previous studies have suggested that the four commercially
62 important species cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting
63 (*Merlangius merlangus*) and plaice (*Pleuronectes platessa*) all make use of recurrent
64 spawning grounds in the North Sea which may be linked to such hydrographic features.
65 In the southern North Sea cod spawns in relatively cool water (5-7°C) beyond the 32
66 isohaline (Aurich 1941). North Sea cod appears to have four distinct spawning grounds, the
67 Southern and German Bights, the southern and eastern flanks of Dogger Bank and off
68 Flamborough (Aurich 1941; Lelièvre et al. 2010; Daan 1978). The recurrent use of the latter
69 area could, however, not be confirmed from findings of a more recent survey in 2004 (Fox et
70 al. 2008). Further north, ripe and running cod have been observed on the Great Fisher and
71 Ling Banks as well as in the coastal areas (<100 m depth) of Scotland (Graham 1934;

González-Irusta and Wright 2016a). In the 2000s the main cod spawning grounds in the northern North Sea were found off the north and east Scottish coasts and east of Shetland towards Viking Bank (González-Irusta and Wright 2016a). Cod in the North Sea do not appear to be a single stock as recent genetic evidence indicates that fish in the deeper northern waters east of Shetland are genetically distinct from other North Sea populations (Heath et al. 2014). In the northernmost North Sea, haddock spawning predominates in the Atlantic influenced water of the deeper outer shelf, (González-Irusta and Wright 2016b; Heath et al. 1994). Haddock rarely spawns in the southern North Sea, spawning has only been extending as far south as the German Exclusive Economic Zone (EEZ) during a pulsed recruitment (Aurich 1941). In the North Sea, haddock egg production appears highest outside the Moray Firth and east of Orkney, though the eggs and larvae spawned to the west of Scotland are advected into the North Sea (Heath and Gallego 1998) and the two regions are treated as one stock for management purposes (ICES 2015).

North Sea whiting is divided into two genetically distinct northern and southern spawning populations (Charrier et al. 2007). This species is among the most prolific spawners in the North Sea, and it has both individually and collectively, an extended spawning period (Aurich 1941). Compared to cod it appears to spawn in warmer water, having an optimum of 5–8°C, and eggs can be found in the southeastern inshore areas (Lelièvre et al. 2010). The main centres for egg production of the southern population are on the western side, off Flamborough, south of the Dogger Bank and in the Southern Bight, while the northern population has its centre south of Shetland (Loots et al. 2011b).

North Sea plaice spawns in a large area of the southeastern North Sea, from the Southern Bight northwards through the German Bight and along the coast of Jutland (Taylor et al. 2007). On the western side of the North Sea, plaice eggs have been found from Flamborough up to the Moray Firth and further northeast off Shetland. The southwestern populations of

197 plaice appear to spawn mainly in the Southern Bight and partially in the eastern English
198 Channel (Houghton and Harding 1976; Hunter et al. 2004). Generally plaice spawns further
199 offshore than most other flatfish species, with the main egg production observed 50-200 km
200 offshore, in salinities >32 (Rijnsdorp 1989). Freshwater from the river plumes apparently has
201 a strong effect on spawning outside the core areas (Lelièvre et al. 2014). The location of the
202 spawning areas is thought to offer good connectivity to inshore, spatially limited, soft
203 sediment nursery grounds (Hufnagl et al. 2013).

204 Life-cycle closure requires a succession of suitable habitats and appropriate mechanisms for
205 transiting between them (Petitgas et al. 2013). There are concerns that predicted climate
206 change may not only affect reproduction directly but also affect early life stage habitats and
207 the connectivity between them (Collins et al. 2013). The changes would have a series of
208 direct and indirect effects, taking place on scales ranging from individuals to populations. It
209 has already been seen that North Sea fish distributions have responded to rising sea
210 temperatures (Perry et al. 2005) whilst changes in wind patterns and restricted transport of
211 *Calanus finmarchicus* into the North Sea have been implicated in cod recruitment (Rindorf
212 and Lewy 2006; Fromentin and Planque 1996). Under climate change the location of salinity
213 fronts, which may direct spawning, could also change (Collins et al. 2013; Perry et al. 2005).
214 Such changes may be especially detrimental for fish species on the southern edge of their
215 range, while other species may be able to extend into the North Sea (Dulvy et al. 2008;
216 Planque and Frédou 1999). Many North Sea stocks have also suffered decades of overfishing,
217 leading to low spawning stock biomasses (SSBs) and truncated age structures. Such stocks
218 may have reduced resilience against changes in the abiotic environment (Ottersen et al.
219 2006). Other human activities may put additional stress on spawners and their offspring,
220 particularly in a heavily industrialized area like the North Sea, containing nearly a thousand
221 active above- and sub-surface structures (De Groot 1996; OSPAR Commission 2014). Except

122 for specific accidents these structures, may, however, only be local disturbances and may
123 even serve as habitat (Løkkeborg et al. 2002; Fujii 2015). Other disturbances might come
124 from seismic exploration which nowadays uses airguns that cause direct physical damage in a
125 much narrower zone than the explosives used in the past (5 m, McCauley et al. 2000). Effects
126 on adults may rather be indirect, causing avoidance of approaching survey vessels. Since
127 seismic surveys are not supposed to be undertaken during periods of fish spawning, or are
128 supposed to use mitigation measures such as soft-starts (Smithies 2014), knowledge of the
129 extent and timing of spawning is essential for proper Environmental Impact Assessment
130 (EIA). Therefore, evaluating the overlap between intense seismic operations and spawning
131 grounds is a normal requirement for EIAs undertaken before seismic operations commence.
132 In 2004 and 2009, dedicated surveys and additional sampling during routine surveys were
133 coordinated by ICES, affording the possibility to examine fish spawning using egg
134 distribution data separated by 5 years.

135 Here we use the egg distribution of the four most abundant species, cod, haddock, whiting
136 and plaice in order to (i) construct statistical models, relating the spawning habitat inferred
137 from stage I eggs, up to the onset of gastrulation, to the abiotic environment; (ii) examine
138 how distribution patterns changed over time by constructing interpolated distribution maps
139 and by statistically comparing the distribution of the successive egg development stages; (iii)
140 evaluate to which extent spawning distribution overlaps with industrial activities and how
141 these, in concert with climate change, may affect future spawning distribution and success.

142 **Materials and methods**

143 **Survey design and field sampling**

144 Sampling was carried out across the North Sea (Fig. 1a) by five participating countries, either
145 during the annual International Bottom Trawl Survey for the first quarter (IBTS 1Q) or in
146 dedicated surveys between the 16th February and 23rd of March 2004 and between 17th of
147 January and 6th of March 2009 (Table 1).

148 The samples were taken with Gulf III/Nackthai (Gehringer 1962; Nellen and Hempel 1969),
149 Gulf VII (Nash et al. 1998), BONGO (Posgay and Marak 1980) and WP2 (Fraser 1968;
150 Tranter 1968) nets, covering the entire North Sea from 51.5°N to 62°N. The Gulf and
151 BONGO nets were deployed in double oblique hauls, while the WP2 was deployed in vertical
152 hauls, in both cases down to five metres above sea bottom or a maximum of 100 m depth.
153 Double oblique hauls lasted at least 10 minutes with multiple hauls ensuring the minimum
154 deployment time in shallow water (ICES 2008). To determine cod-like eggs to species level,
155 single eggs without oil globules and diameters of 1.1-1.75 mm (Fox et al. 2008) or 0.97–
156 1.89 mm (Lelièvre et al. 2010) were fixed for later genetic analysis, either in 96% ethanol
157 (Fox et al. 2008) or in a pigment preserving Battaglia-solution containing buffered 0.864%
158 formalin, BHA (butylated hydroxyanisole), EDTA (ethylenediaminetetraacetic acid) and
159 monopropylene glycol and ascorbic acid (Mastail and Battaglia 1978; Bigot 1979).

160 The locations of installations for oil extraction, seismic survey areas and the outlines of
161 exclusive economic zones were extracted from public online databases (Fig. 1b, OSPAR
162 Commission 2014; Ministerie van Economische Zaken 2015; Oljedirektoratet 2015). Depth
163 and shoreline data were downloaded from NOAA databases (NOAA (NGDC) 2016a; NOAA
164 (NGDC) 2016b).

165

166

Egg and larvae identification

Subsamples of at least 100 eggs in the desired size range (>1.16 mm, Russell 1976) were staged (Ryland et al. 1975; Geffen and Nash 2012) and visually identified to the lowest possible taxonomic level (Munk and Nielsen 2005; Russell 1976). Preserved cod-like eggs were identified either with TaqMan probes (Fox et al. 2008) or cytochrome *b* PCR–RFLP (Lelièvre et al. 2010). Accuracy of TaqMan probes is $>98\%$ for cod, haddock and whiting (Taylor et al. 2002) while cytochrome *b* PCR–RFLP confirmed 98% of visual identifications for late-stage cod eggs and 71% for late-stage whiting eggs (Lelièvre et al. 2010). The identified gadoid eggs were assigned to each species according to the proportion obtained from genetic analyses. For stations where this was not possible, the proportion in 2004 was derived from a multinomial Generalized Additive Model (GAM) over the whole survey area (Fox et al. 2008) and in 2009 from the average proportion for the other stations in the same ICES square. Counts of fish eggs were raised by the fraction of the whole sample examined and then converted to density (eggs m^{-2}), by dividing by the sampled volume and multiplying by the sampled depth.

Geostatistics

Hydrographic data were obtained from CTD hauls during the survey and augmented with data from the ICES oceanographic database (ICES 2009). After pre-screening for erroneous measurements, density anomalies σ_t ($\text{kg m}^{-3}-1000$) were calculated from temperature and salinity according to UNESCO standards (Millero and Poisson 1981) using the R package *oce* (Kelley 2013). To calculate the density gradient, an experimental variogram for σ_t was calculated in Surfer 10 (Golden Software 2011) and a linear theoretical variogram model fitted to the experimental variogram, using least square regression. Using ordinary kriging, the density anomaly was then interpolated onto a regular grid of $0.25^\circ \times 0.25^\circ$ and

subsequently smoothed to half that grid resolution. From the interpolated horizontal density anomaly the density gradient in $\text{g m}^{-3} \text{ n.mi.}^{-1}$ was calculated using the formula (Golden Software 1999):

$$(1) \quad \|\vec{g}\| = \sqrt{\left(\frac{Z_E - Z_W}{2\Delta x}\right)^2 + \left(\frac{Z_N - Z_S}{2\Delta y}\right)^2}$$

Where \vec{g} is the density gradient, Z_E and Z_W are adjacent grid points in East-West direction; Z_N and Z_S are adjacent grid points in North-South direction, Δx and Δy the distances in either direction, respectively.

For visual representation, temperature and salinity were interpolated on a $1 \text{ n.mi.} \times 1 \text{ n.mi.}$ grid using the R package gstat (Pebesma 2004). Analogous to the procedure for σ_t an experimental variogram was calculated and a Gaussian, exponential or spherical theoretical variogram was fitted to the experimental variogram using least-square regression and eye-fit. The chosen model was then used for the interpolation. Average temperature and salinity data for the 2000s was also interpolated following the same procedure. However, the value plotted here was the variation, to visually compare the distribution of stage I fish eggs with the variation of hydrography.

Similarly, data for each egg development stage were split into presence/absence and log-transformed non-zero abundance and then interpolated using an ordinary kriging procedure on the default grid in gstat (Pebesma 2004). The values for abundance were then weighted with the probability of occurrence on a cell-by-cell basis and the final maps created by kriging onto the same $1 \text{ n.mi.} \times 1 \text{ n.mi.}$ grid that was used for hydrography.

213 Statistical comparisons of egg density distributions between stage I and the later stages were
 214 performed using the Syrjala test in the R package ecespa (de la Cruz 2008). The Syrjala test
 215 computes a modified two-sample Cramér–von Mises test for a difference between the
 216 cumulative distribution functions of two populations (Syrjala 1996). As the test is sensitive to
 217 where the coordinate system has its origin, it is performed once for each of the four corners of
 218 the hypothetical rectangle encompassing all sampling sites and then averaged. Although the
 219 test is insensitive to sample size, each sample was transformed to ‰ of the sum of the
 220 respective stage before conducting the test.

221

222 **Modelling spatial autocorrelation**

223 Spatial autocorrelation and average patch size were modelled with Moran’s eigenvector maps
 224 (MEMs) using the R package pcnm (Legendre et al. 2013). A truncated distance matrix was
 225 computed by converting all distances farther than the longest distance between immediate
 226 neighbours to four times that value (Borcard and Legendre 2002). Since there are no
 227 interactions in the population of fish eggs, only the MEMs with positive eigenvalues were
 228 retained. Before running a global test on all MEMs with positive eigenvalues the hellinger-
 229 transformed abundances were detrended to remove any spatial trend. Individual Moran’s
 230 Eigenvectors (MEVs) were selected by regression-based forward selection with the R
 231 package packfor (Blanchet et al. 2008; Dray et al. 2013) using p-value and adjusted r^2 as
 232 stopping criteria. Similar to Loots et al (2010a) the threshold p-value was set to a low 0.002,
 233 to avoid building too complex spatial models. The spatial scale was then determined by first
 234 computing a Gaussian variogram for each MEM (Bellier et al. 2007). Then the selected
 235 MEMs’ eigenvalues were plotted against these ranges and subdivided into sub-models for a
 236 fine, medium, medium-broad and broad scale.

237

Explanatory models

To examine the relationships between the distributions of stage I eggs and the abiotic environment, data from both years were used to construct a generalized additive mixed model (GAMM) with the R package gamm4 (Wood and Scheipl 2014; Wood 2006). As for the kriged distribution maps, separate models were constructed for presence/absence and non-zero abundance, resulting in a hurdle-model. Potential independent variables were temporal (year, day of the year), bathygraphic (bottom depth), hydrographic (temperature, salinity, and σ_t -gradient; from the surface and bottom) and the selected MEVs. These variables were examined for collinearity with pair plots and variance inflation factors (AED, Zuur 2010), entailing the exclusion of the year. Hydrographic values were taken from the CTD casts taken at the locations of the individual samples or, if not available or erroneous, were extracted from the interpolated surfaces. The measurements from 5 m depth and the bottom were strongly correlated. Instead of excluding one or the other, separate models using either surface or bottom measurements were constructed and compared. MEVs were treated as random effects, while the day of the year (=year day), bottom depth and the hydrographic covariates were the fixed-effects. Using either presence/absence in a binomial model with a logit-link or log-transformed non-zero egg densities in a Gaussian model with identity-link as response, the general form of the GAMM was (Wood 2006; Höffle et al. 2014):

$$(2) \quad y_i = \beta + f_1(x_{1i}) + f_2(x_{2i}) + \dots + f_n(x_{ni}) + Z_i b + \varepsilon_i$$

y_i being the response, β the intercept, f_i the smooth functions for the fixed effects x_k , b a random effects coefficient vector from the matrix Z_i and the residual error vector ε_i .

260 The risk of over-fitting the individual models was reduced by restricting the degrees of
 261 freedom to four and by using the Bayesian Information Criterion (BIC, Schwarz 1978) as an
 262 indicator of improvement during the backward selection of the optimal models. Initial models
 263 contained hydrographic measurements from either the surface (5 m) or the bottom depth.
 264 Following the optimization of these models the decisions between either surface or bottom
 265 models were based on BIC, Akaike's Information Criterion (AIC, Akaike 1974) and in case
 266 of disagreement between the two on the predictive power of the models. Formal assessment
 267 of the goodness of fit, since not possible from the GAMM itself (Wood 2006; Zuur et al.
 268 2009), was done by estimating the deviance explained from a generalized additive model
 269 (GAM) using the same fixed-effects covariates (Gilman et al. 2012). Post-hoc testing
 270 included an evaluation of the random effects' contribution, using the residuals from the GAM
 271 as response (Wood 2006). Hereby, linear fixed-effects and mixed models are compared, by
 272 using a constant parameter and in the mixed model the random effects. The two models are
 273 then compared by AIC, BIC and the log-likelihood ratio test.
 274 The effect of the random covariates on the spatial autocorrelation was evaluated by Moran's I
 275 correlograms on the models' residuals, setting a separation distance of 0.7° for non-zero egg
 276 densities of cod and plaice, 2.1° for all other models, corresponding to the maximum distance
 277 between nearest neighbours (Diniz-Filho et al. 2003; Borcard et al. 2011). The number of
 278 lags to cover the entire study area was then 15 and 5, respectively. *P*-values were adjusted
 279 using Holm's correction (Borcard et al. 2011).
 280 The performance of individual fixed covariates was evaluated using three different indicators.
 281 Firstly, by dropping each covariate individually and then calculating the log-likelihood ratio
 282 between the reduced model and the model selected in the fitting process. Secondly, by
 283 computing the ROC AUC (Receiver Operating Characteristic Area Under the Curve) for
 284 binomial and the r^2 between response values predicted from individual covariates and the

observations for Gaussian models using the R package MuMIn (Barton 2013). Lastly, partial linear regression and adjusted r^2 were used to partition the explained variation explained by the individual covariates using the R package vegan (Oksanen et al. 2013; Peres-Neto et al. 2006).

Results

Hydrography

In both years hydrography was characterized by a pool of relatively warm ($>7^{\circ}\text{C}$) and saline (>34.5) water in the northern and central North Sea and cooler, fresher water along the margins, which was more pronounced in the East (Fig. 2). Salinity (Figs 2b, d) as well as density gradients (max. $4.3 \text{ g m}^{-3} \text{ n.mi.}^{-1}$ off Norway) were steeper on the eastern side of the North Sea. Surface hydrography was more structured than at the bottom. The main difference between 2004 (Fig. S1) and 2009 (Fig. S2) was that in the southern North Sea water $\leq 6^{\circ}\text{C}$ extended further westwards in 2009. The water in the German Bight was more than 1°C colder than in 2004 and salinity gradients from coastal to offshore waters were shallower, particularly north of the Frisian Islands where a prominent plume of relatively fresh (≤ 34.25) water extended far offshore. North of 57°N the situation was the opposite with the salinity gradient steeper in 2009 (Fig. S2) than 2004 (Fig. S1).

Spatial structuring

The threshold for truncating the distance matrix was 2° . Of the MEMs, 355 were found to have positive eigenvalues. Two of these were significant for cod, four each for haddock and plaice and one for whiting. When plotting eigenvalues against the variogram range, there were four distinct groups (Fig. 3), on ranges of 0-40 n.mi. (fine), 40-75 n.mi. (medium), 75-100 n.mi. (medium-broad) and above 100 n.mi. (broad).

Egg distribution

Stage I egg densities on the scale of the entire North Sea were in both years in the same general areas (Fig. 4). High egg densities of cod (Fig. 4a) and plaice (Fig. 4p) were found in the Southeast, along the continental coast, extending as far north as Viking Bank. Whiting and haddock were more common in the western part. The centre of egg densities for haddock was limited to the Northwest (Fig. 4f), two patches on either side of the Fladen Ground and a third, smaller, patch outside the Firth of Forth. Peak densities of whiting eggs also occurred in three locations but they were farther apart. One centre of abundance was east of the Shetland Isles (Fig. 4k) around the Forties, the second, larger, area was between Flamborough and the Dogger Bank and a third area was in the Southern Bight.

The overall pattern in the development over time was one of decline and dispersal. For cod and whiting (Figs 4a-e, 4k-o) this process appeared to be quicker compared with haddock and plaice with a sharp drop in egg densities between stages I and II and a lower rate of decline thereafter. For haddock and plaice the peak densities did not decline as quickly (Figs 4f-j, 4p-t), densities of the same magnitude as in stage I were still observed in stages IV and V (Figs 4i, 4t). However, the area covered by high densities shrank and in the case of haddock divided into several smaller well-separated patches.

The main differences between the years (Figs S3, S4) were that the centres of abundance for cod and plaice were further north and offshore in 2004 than in 2009 and that the rate of dispersal differed between the years for each individual species. In 2004 high cod and plaice densities covered a larger area (Figs S3a-e, S3p-t), from the transition area between the Bights up to the southern edge of the Norwegian trench. For cod in 2009 this area was smaller, more inshore, off the Frisian Islands, while egg densities were higher in the northern patch around Viking Bank (Fig. S4a-e). For plaice the overall location was similarly changed,

extending along an east-west axis rather than a north-south axis, but the extent of the area was similar to 2004. Peak densities of cod eggs and the area covered with such densities, quickly declined in 2009, while in 2004 high densities were still found in stage III (Fig. S3c). There was no such difference for plaice, although in later stages (Figs S3s and S3t) the location of peak densities was similar to 2009. High egg densities of haddock covered much larger areas in 2004 (Figs S3f-j) than in 2009 (Figs S4f-j) and the distribution pattern did not disperse as quickly and completely. Whiting egg densities were generally lower in 2009 than in 2004 (Fig. S4k-o) but there was little difference in how quickly the eggs dispersed. However, the overall pattern was different (Fig. S3k-o) with high densities in the Southern Bight in 2009 while in the earlier year the centres of abundance were off Flamborough and east of Shetland.

The Syrjala-test did not fully confirm the patterns suggested by the interpolated maps (Table 2). The distribution patterns of stage IV and V were more often dissimilar from stage I than those of earlier stages, but that pattern was not consistent across species or years. Although stage IV was significantly dissimilar for all species when comparing mean distributions, it never was for whiting in any of the single years. Similarly, the distribution of stage V was significantly different for all species in 2004, but not in 2009 or for mean distributions. Stage III never exhibited significant dissimilarity to stage I, although there were three cases of significantly different distributions between stages I and II.

Explanatory models

The overall trends in the explanatory models were twofold. Firstly, the best fitting models for non-zero egg density tended to be more complex than those for the probability of occurrence (Table 3, Figs 5, 6). Secondly, although the difference was marginal, three out of four models exhibited a better fit when using hydrographic measurements at the bottom for the probability

of occurrence, while for egg densities it was the opposite. Deviations explained by the corresponding GAMs ranged between 15% for the density of stage I cod eggs and 57% for the presence/absence of haddock eggs. The models for these two species also consistently retained the least fixed-effects covariates (3) for both cod models and the most (5) for both haddock models (Table 3).

Bottom depth and year day were the only fixed-effects covariates retained in every model. They also exhibited similarly shaped relationships for three of the four species (Figs 5a, b). Cod, Haddock and Whiting exhibited an increasing trend towards the end of the period. Plaice differed from the other species, exhibiting a dome shaped relationship between days 30 and 70. The relationships of cod and plaice egg densities with the year day were of similar shape and peaked earlier than their probabilities of occurrence (days 45 and 35; Fig. 6a). Whiting egg densities exhibited an early and a late peak around days 20 and 80, respectively. Haddock egg densities were linearly and positively related to the year day.

Probabilities of occurrence for cod and plaice exhibited overall decreasing trends of similar shape with peak probabilities at ca. 50 m (Fig. 5b). Haddock exhibited a similar pattern, but shifted towards greater depths, with a peak at around 100 m and an increasing trend towards the end of the observed depth range. The probability of finding stage I eggs of whiting declined with increasing depth, becoming zero at ≥ 150 m (Fig. 5b). Relationships between egg densities and bottom depth were of similar shape for cod, whiting and plaice, with peaks at shallower depth than peak probabilities of occurrence (Fig. 6b). Haddock egg densities exhibited a Gaussian distribution around 100 m.

Other than for time and depth, the relationships between the probability of presence and the hydrographic covariates were more species specific with no consistent patterns between any two species. Temperature did not contribute to the model for the occurrence of cod eggs and exhibited negative and positive trends for plaice and whiting, respectively (Fig. 5c). For

385 haddock the probability of finding eggs was high across the temperature range, except for a
386 local decline around 6°C. Unlike for probability of occurrence, the smooth terms for egg
387 densities related to hydrographic measurements exhibited similarities between two or more
388 species. Haddock consistently differed from the other species, exhibiting linear or near-linear
389 increases in egg densities in relation to year day, salinity and density gradient. Temperature
390 contributed to all models for egg density with the peak occurring as low as ca. 5°C for plaice
391 and as high as 9°C for whiting. The smooth terms for cod and plaice were similar in shape
392 and both egg densities peaked at nearly the same temperatures. Observations at either end of
393 the observed temperature range were few and therefore have wide confidence intervals.

394 Salinity contributed to the model for the probability of occurrence of cod eggs (Fig. 5d) but
395 did not contribute to the model for egg densities (Fig. 6d). Cod probability of occurrence
396 exhibited a weakly declining trend towards higher surface salinities, while haddock was
397 strongly positive related to bottom salinity. Salinity was only retained in the models for egg
398 densities of whiting and plaice, exhibiting similar shapes of the smooth terms, with peaks at
399 the lower end of the range and at salinities of 34. Haddock eggs were only observed in a
400 narrow salinity range and the trends of probability of occurrence as well as egg densities were
401 strongly positive. The density gradient was retained in the presence/absence models for
402 haddock and whiting (Fig. 5e) and the egg density models for these two species as well as for
403 plaice (Fig. 6e). Egg densities of all three species were linearly related to density gradients.

404 Across all species the relationships to the MEVs describing spatial autocorrelation were
405 linear or dome shaped (Figs S5 – S8). Spatial autocorrelation in the residuals was by a factor
406 of 1.5 to 7.5 lower than in the data used for fitting. However, on the first lag it remained
407 significant (Table 3).

408 Predictive power of the selected models was highest for the presence/absence of haddock, the
409 egg density model of whiting and lowest for both models for cod (Table 4). Individual

410 covariates with high predictive power strongly affected the log-likelihood ratios as well
 411 (Table 5). Concerning explained variation this consistency in performance of individual
 412 covariates was limited to cod (Table 6). The variation explained by the fixed-effects
 413 covariates was lowest for cod and highest for haddock. The highest percentage of explained
 414 variation in presence/absence was related to bottom depth for plaice and year day for all other
 415 species. For the egg densities the highest percentage of explained variation was related to
 416 temperature for cod, salinity for haddock, and density gradient for whiting and plaice,
 417 respectively. This increased importance of hydrographic variables in the egg density models
 418 was not reflected in the predictive power or the log-likelihood ratios where these covariates
 419 were usually weaker than either year day or bottom depth.
 420 The comparison between the GAMMs and their corresponding GAMs using only the fixed-
 421 effects covariates revealed that the MEVs only contributed significantly to the models for
 422 whiting (Table 7). However, even for whiting the GAM was more parsimonious, as the AIC
 423 and BIC was for all GAMs lower.

425 **Comparison with decadal hydrography and oil installations**

426 Averaged over the 2000s the variation in bottom temperature exhibited a range of interannual
 427 variability between $<1^{\circ}\text{C}$ and $>1.6^{\circ}\text{C}$ (Fig. 7a). The lower part of this range was found in
 428 large areas of the central and southern North Sea, while the rest of the North Sea proper
 429 exhibited intermediate variation. High variability was primarily indicated on the northern
 430 margins of the North Sea and between the Shetland and Orkney Isles as far south as the
 431 Moray Firth. High egg densities across all four species were primarily found at the
 432 boundaries between the areas of low, intermediate and high variability. The mean density of
 433 stage I eggs across all species, compared to the distribution of oil extraction and seismic
 434 survey areas in the eastern North Sea showed that at this time of the year areas of high egg

435 densities primarily overlapped with the oil industry in the southeastern North Sea in the
436 Dutch and German EEZs (Fig. 7b).

437

438 **Discussion**

439 The results of the present study indicate that presence/absence and non-zero abundance of
440 cod, haddock, whiting and plaice eggs are primarily governed by different environmental
441 variables. Presence/absence was mainly linked with the day of the year as well as bottom
442 depth whilst non-zero abundance was linked to one or more of the hydrographic covariates.
443 Overall, the spawning of cod and plaice appears more common in the southeastern North Sea,
444 while spawning of haddock and whiting were concentrated in the western areas, and in the
445 case of haddock further limited to the northern North Sea. The overall spawning areas seem
446 to have remained stable, compared to historical observations. However, the, smaller, actual
447 spawning grounds used within those areas varied between the two years surveyed depending
448 on prevailing conditions.

449

450 **Egg distribution**

451 Where spawning locations persist over many years their use must allow sufficient offspring
452 to survive to sustain the population size (see Hufnagl et al. 2013). Our observations of
453 geographically relatively stable spawning areas contrast findings for other species such as,
454 e.g. mackerel (*Scomber scombrus*, Beare and Reid 2002). However, even for mackerel the
455 spawning occurs mainly along the shelf-break and this location may be linked to patterns in
456 secondary production driven by internal waves (Sharples et al. 2009). Areas of the North Sea
457 where high abundances of cod, haddock, whiting and plaice eggs were found are consistent
458 with earlier studies (Coull et al. 1998; Heath et al. 1994). However, their extent at higher
459 population levels might be greater and at the present time the maximal extent of the spawning

460 areas may be better indicated by egg occurrence (Brander 1994). The overall better fit for the
 461 presence/absence models when including hydrographic measurements from the bottom rather
 462 than from the surface may be due to the generally demersal behaviour of the adult fish. On
 463 the other hand the better fits for egg densities using surface hydrography may be based in the
 464 distribution of pelagic eggs in the upper part of the water column (Coombs et al. 1990;
 465 Fritsch 2005). After rising to the surface layer, eggs will be advected from the spawning site.
 466 However, in the observed temperature range the eggs develop to the end of stage I within a
 467 few days (Thompson and Riley 1981; Geffen and Nash 2012). At common winter current
 468 velocities (Sündermann and Pohlmann 2011), dispersal during that time should have been on
 469 about the same scale as the survey. This is supported by recent studies on the distribution of
 470 mature adults which largely corroborate the finding from the egg surveys (González-Irusta
 471 and Wright 2016a; González-Irusta and Wright 2016b; Loots et al. 2011b) The only major
 472 difference was that the northern core spawning grounds of whiting extended further south
 473 than was observed in the egg surveys (Loots et al. 2011b). Therefore, the distribution of stage
 474 I eggs observed in 2004 and 2009 may be considered a reliable source of information on
 475 spawning distribution.

476

477 **Relationship with the abiotic environment**

478 Compared to Otto and Zimmermann (1990) and the studies underlying that review (Goedecke
 479 et al. 1967; Tomczak and Goedecke 1962), the overall pattern of hydrography in the North
 480 Sea in 2004 and 2009 was not much changed since the 1960s. Patterns were also similar
 481 between the sampled years with the main differences in temperature and salinity occurring
 482 south of 57°N. A major difference between the two survey years were the higher egg
 483 densities of whiting in the Southern Bight in 2009. The difference in egg densities in the
 484 Southern Bight correlates with the hydrographic differences, as whiting may have spawned

485 across the boundary between the cool, low salinity coastal water and the warmer water from
486 the South, corresponding to the species preferences (Aurich 1941). In the southern North Sea
487 a comparable data set is available from a series of surveys using the Continuous Underway
488 Fish Egg Sampler (CUFES, Lelièvre 2010). In this study high egg densities of all species
489 were found in the Southern Bight in 2006 and 2008, but to a lesser extent in 2007 (Lelièvre et
490 al. 2012). In 2006 low salinity was not restricted to the German Bight and the interface
491 between fresh and saline water was further offshore, resembling the situation in 2009. From
492 the comparison of the years we deduce that a more seaward position of the boundary between
493 freshwater influenced areas and marine water may attract more spawning fish to the area.
494 The present observations on cod egg distribution are consistent with Aurich (1941) and
495 Brander (1994). The latter author identified the western-central North Sea (2°W-2°E and
496 52.3-56°N) as a minor contributor to the spawning of cod, and the German and Southern
497 Bights as major contributors in alternating periods, 1948-1956 and 1958-1972, respectively.
498 In 2004 and 2009, the distribution of cod eggs in the Southern Bight was limited to a few
499 patches, while in the German Bight cod eggs were widespread, similar to the pattern
500 described by Brander (1994).
501 Densities of cod eggs peaked in areas shallower than 100 m, corresponding to results of
502 previous ichthyoplankton studies (Munk et al. 2002) and in line with González-Irusta and
503 Wright (2016a) who reported that the abundance of cod in spawning condition declined at
504 more than 125 m water depth (González-Irusta and Wright 2016a). The temperature (ca. 4°C)
505 at these locations corresponded to the distribution of spawners which declined when
506 temperatures increased to above 5°C (González-Irusta and Wright 2016a). Cod larvae tend to
507 aggregate at or slightly inshore of a frontal system (Munk et al. 1999) but for the
508 presence/absence and abundance of cod eggs the gradient in water density did not appear to
509 be an important covariate in our analyses. Hence, the aggregation around fronts may only

510 become established by selective processes or behaviours taking place in the larval stage.

511 Patterns of egg production were not entirely consistent with predictions based on the catches

512 of mature female cod in research surveys (Fox et al., 2008). This was particularly the case in

513 the northern North Sea where the bulk of the cod stock is presently located and where high

514 egg production would be expected. Cod in the northern population centred around Viking

515 Bank spawn several weeks later than those in the southern North Sea (González-Irusta and

516 Wright 2016a), which may call for changes in the timing of future ichthyoplankton surveys.

517 The greatest spawning concentrations of haddock have historically been reported from the

518 plateau between the Orkney-Shetland Isles and Norway in water deeper than 100 m

519 (Thompson 1928). A statistical model developed for spawning haddock west of Scotland also

520 indicated a decline at greater depths, which corroborates the egg-based model in the present

521 study (González-Irusta and Wright 2016b). Spawning aggregations have also been reported

522 east of the Moray Firth, at the Buchan and Farne deeps, the Gut and the Fisher Banks. Saville

523 (1959) found haddock eggs to be widely distributed across the northern North Sea from the

524 Scottish coast to the Norwegian deeps except for the Moray Firth and an area around the

525 Fladen Ground. The low egg densities around the Fladen Ground appear a consistent feature,

526 as they were also noted by Damas (1909), González-Irusta and Wright (2016b) and in the

527 present study. The extent of haddock eggs found by Heath et al (1994) in 1992 was

528 comparable with that of Saville's study, although eggs were concentrated further north and

529 west. Heath and Gallego's (1998) study estimated high egg production from mature fish for

530 the Moray Firth, the Scottish east coast and Shetland Isles, which is reflected in the results of

531 the two surveys. However, their model did not predict high abundances to the immediate east

532 of the Shetland Isles, which were present in 2004, 2009 and earlier egg surveys. High

533 abundances of haddock eggs south of the Moray Firth were only found in 2004. In earlier

534 plankton surveys Heath et al. (1994) found a spatial segregation of late stage cod and

535 haddock eggs, in colder North Sea water and on the warmer outer shelf, respectively. These
536 findings support the suggested preferences for different zones of a frontal system between
537 these gadoids (Munk et al. 1999). More common occurrence and higher abundance of
538 haddock eggs on the offshore side of a frontal system, was also seen in the relationships to
539 the environmental covariates. Observations of haddock eggs were limited to a narrow part of
540 the species' salinity range (30-36, Laurence and Rogers 1976). Within the observed range,
541 the probability of occurrence as well as egg densities increased. Likewise the warmer
542 offshore water, where a local peak was found at 7°C in the present study, falls within the
543 species' temperature range (4-10°C, Laurence and Rogers 1976). Similarly, spawning
544 haddock reached peak probability of presence and abundance at 7°C and exhibited peaks at
545 salinities >34 and >35, respectively (González-Irusta and Wright 2016b). Density gradients in
546 the northern North Sea were lower than in the South. Nevertheless, they positively affected
547 the abundance and to a lesser extent the occurrence of haddock eggs. This may be related to
548 the observed high numbers of eggs on the oceanic side of the front between the Atlantic and
549 the North Sea water in the northwestern North Sea (Heath et al. 1994).

550 It has been suggested that the whiting population consist of two stocks in the North Sea, one
551 east of England and one east of the Shetland Isles (Charrier et al. 2007). Such separation is
552 consistent with our findings. The preferred habitat of adult whiting can be characterized by
553 shallow depths and relatively high winter temperatures of 6-9°C (Damas 1909). This
554 preference was apparently reflected in the higher probability to find whiting eggs as well as
555 higher egg densities in the upper temperature range. Egg abundance peaked not only at
556 temperatures >7°C but also at sub-optimal temperatures of 4°C, but still within the thermal
557 range for egg survival (Pova et al. 2011). Probability of occurrence and abundance peaked
558 in the 20-40 m range identified as preferred depth range for spawning by Aurich (1941). The
559 likelihood to find whiting eggs increased at high density gradients, while the egg densities

declined, partially corroborating the findings of Munk et al (1999), who found that whiting eggs were uncommon at central parts of fronts. Whiting has a long spawning period, from February to June with increasingly later spawning at higher latitudes (Hislop 1984). Hence, the earlier sampling period in 2009 may partially explain the difference to 2004, particularly in the northern spawning grounds east off Shetland. In 2009 spawning east of Shetland may not have begun at the time of the survey. However, in 2004 stage IV and V eggs were abundant in the North, while early stages occurred more in the southern North Sea, contrary to the observations by Hislop (1984) and Aurich (1941). As individual whiting spawn many batches over a period between 1.5 and 2 months into late spring (Hislop 1984), the 2004 survey may have sampled the early stages of a later spawning batch in the South, while in the North the previous batch was sampled in the later stages.

The relatively homogenous distribution of plaice eggs in the German Bight and along the Danish coast, particularly in 2004, is a good representation of this species' large spawning area in the southern North Sea and English Channel (Aurich 1941; Metcalfe 2006). Moray Firth, Firth of Forth and the area off Flamborough Head are further suitable for plaice spawning (Loots et al. 2010b) and some eggs were found there, in earlier surveys (Aurich 1941) and in the present study. To develop successfully, plaice eggs need a temperature range of 2-8°C (Wegner et al. 2003), which was reflected in the above average abundance of eggs at 4-6°C. The probability of finding plaice eggs was similarly highest at the lowest observed temperatures and declined linearly over the observed range, indicating that within the species' thermal range the lower part is preferred (Wegner et al. 2003). The high densities of plaice eggs at salinities ≥ 34 corroborated earlier studies indicating high salinities as optimal for plaice eggs (Aurich 1941; Cushing 1990). The linear relationship between egg densities and density gradient was negative and had a similar slope to that for whiting. This result

584 supports earlier studies indicating more offshore spawning grounds than other flatfish
585 (Lelièvre et al. 2014).

586 Overall, egg densities declined quickly between stages I and II and at a lesser rate towards
587 later development stages. However, distribution patterns remained largely the same up to
588 stage IV. Therefore, one can assume that the decline was primarily driven by the high
589 mortality of fish eggs (Bunn et al. 2000), and that mortality rates were similar across the
590 North Sea. Contrary, dispersal may be rather slow. In the southern North Sea, eggs are
591 advected at about 5 km d⁻¹ (Brander 1994), resulting in a transport of around a 100 km from
592 spawning to hatching, based on temperature dependent egg development (Thompson and
593 Riley 1981; Geffen et al. 2006). This slow dispersal may explain why distribution patterns
594 remained similar until the later stages. As indicated by *p*-values in the Syrjala-test,
595 distribution patterns of stages I and III were often more similar than those of stage I and II.
596 This may be due to the difference in duration of development stages. It is less likely to find
597 stage II eggs during a survey, as it is comparatively short (Fox et al. 2003; Geffen et al.
598 2006).

599 Areas with high densities of haddock eggs, similar to densities in stage I, were maintained
600 longer than for cod and whiting. Partially this might be due to a larger contiguous area with
601 high densities to start with. Another factor may be that the distribution of adult haddock in
602 the first quarter changes little (Hedger et al. 2004), suggesting that predators were satiated by
603 a continuous supply of freshly spawned eggs rather than feeding on the less numerous later
604 stages. A similar mechanism may be at work in case of plaice, which also started out with a
605 large area of high densities that shrank but did not disappear over time.

606

607

608

609 **Individual covariates**

610 The greater importance of the hydrographic variables concerning explained variation, and to
611 a lesser extent predictive power and the log-likelihood ratios, in the egg density models
612 contrasts with the findings of earlier studies. In the present study the year day was the most
613 influential covariate in determining presence/absence. However, earlier studies indicated that
614 environmental covariates are more important for defining the boundaries of a population's
615 habitat, rather than the distribution within (Loots et al. 2011a; Loots et al. 2010a). However,
616 it is not without precedent. Although they used a different measure, González-Irusta and
617 Wright (2016a) came to a similar result for the abundance of North Sea cod in spawning
618 condition. In their study, temporal covariates were likewise the most important ones,
619 followed by salinity as the most important hydrographic covariate. Still, the importance of the
620 year day must be interpreted with care, due to the time series being short and the survey
621 periods differing by about three weeks. Longer time series with several samples on the same
622 year day may reduce its influence (e.g. Höffle et al. 2014; Lelièvre et al. 2014). The
623 distribution of populations on the edge of their environmental range may experience a
624 stronger influence of the environment, which may apply to cod and haddock. Haddock is
625 environmentally restricted to the northern North Sea and while distributed across the North
626 Sea, cod still experiences a strong influence of temperature, because the North Sea stock is
627 one of the most southernmost ones (Hedger et al. 2004; Drinkwater 2005).

628 MEMs are a powerful tool to deal with spatial autocorrelation. However, the additional
629 covariates may be penalized in model selection (Loots et al. 2011a). This may be one reason
630 why only the models for whiting exhibited a significant difference in the log-likelihood ratio
631 test, as they only contained a single MEV on the broad scale. Broad scale structures were also
632 those with the most discernible patterns when plotting observations against predictions,

indicating that these structures were likely more important for characterising the spatial distribution of spawning than those on smaller scales.

Long-term change and short-term disturbances

The four species in the present study may be affected in different ways by long-term changes in environmental conditions of the North Sea, potentially compounded by short-term disturbances (Collins et al. 2013; Petitgas et al. 2013). The debate whether recent changes in the distribution of some North Sea species are related to climate change or to changes in local populations is still ongoing (Neat and Righton 2007; Holmes et al. 2014). The present study indicates that effects would be species specific, with cod and haddock experiencing stronger direct effects of rising temperatures (Hedger et al. 2004; Drinkwater 2005). However, Petitgas et al. (2013) highlighted the potential impact of indirect effects on species with specific habitat requirements for spawning grounds or nurseries as well as on the connectivity between these areas. Plaice appears to be particularly vulnerable as spawning grounds are offshore and the, narrowly defined, nursery areas inshore (Hufnagl et al. 2013). North Sea plaice is one of the more southern populations and suitable spawning grounds and nurseries may decrease in size (Petitgas et al. 2013). Connectivity may be affected by accelerated development and changing current patterns through changes in wind and runoff patterns. For the period 1975 to 2006 Hufnagl et al. (2013) observed a decrease in connectivity related to an increase in temperature, for the spawning grounds in the German Bight and in the English Channel, while connectivity for other areas increased. For cod, connectivity may be affected in the opposite way, as climate change may entail more natal retention (Heath et al. 2008). However, other studies suggested a displacement to the North (Rindorf and Lewy 2006). Whiting may also be affected by changes in salinity and subsequently stronger density gradients in its, previously more homogenous, spawning areas (Loots et al. 2011a).

658 While the effects of changes in climate are long-term, short-term disturbances may interact
659 with them. Noise producing activities, such as seismic surveys as well as construction work
660 and the ensuing avoidance reactions, may lead to delays in spawning or avoidance of optimal
661 spawning grounds and therefore interfere with successful connectivity between spawning and
662 nursery areas. Together with minor injuries and their effects on long-term survival such
663 indirect effects of noise pollution are understudied and call for further research (Wahlberg
664 and Westerberg 2005; Payne 2004). Such impacts are considered in the EIA that must be
665 undertaken before seismic surveys are conducted. Where potential impacts are judged serious
666 then mitigation measures must be taken. Mitigation can include restricting the timing of work
667 so it is outside of the spawning season or other measures such as soft-starts for pile-driving
668 and air gun surveys. It is therefore important that up-to-date information is available
669 regarding spawning locations and timing so that offshore exploration and construction
670 activities can be properly controlled. Of the four species in the present study, cod and plaice
671 overlap with areas for seismic surveys, whether for oil exploration or construction work, in
672 the southeastern North Sea (Ministerie van Economische Zaken 2015). Cod may be
673 vulnerable due to its SSB being below B_{trigger} , the biomass triggering management actions,
674 while plaice is vulnerable due to its dependence on successful connectivity between early life
675 stages.

676

677 **Conclusion**

678 Spawning areas appear to be defined by few, time-invariant variables, while centres of
679 abundance within these areas are influenced by the interannual variability of the hydrographic
680 conditions. Explanatory power of the statistical models varied between 15% explained
681 deviation for cod egg density and 57% for haddock egg presence/absence. Models for cod
682 spawning distribution, whether they use eggs or ripe and running adults as response, appear

683 to be difficult to define as even a far larger number of covariates barely yielded double the
684 explained deviation (González-Irusta and Wright 2016a). Considering that the cod stock is
685 currently the most vulnerable one in the North Sea, the investigation of further drivers
686 governing the spawning distribution should concentrate on this species. Performance of
687 individual covariates indicates that the occurrence of spawning in a given location of the
688 North Sea is more dependent on covariates that do not vary over time, as the most important
689 covariates for these models were year day and bottom depth. Contrary, egg densities were to
690 a greater extent governed by covariates that change over time. This suggests that changes in
691 the ocean climate, not exceeding the fishes' physiological limits, may cause centres of
692 abundance to shift within spawning areas that remain the same. Such centres of abundance
693 should be avoided by potentially damaging activities, and aggregate maps of spawning
694 habitats and egg distributions, such as in the present study and Lelièvre et al. (2014), would
695 be valuable tools in the management of marine areas, protecting the successful reproduction
696 of fishes.

697

698 **Supplements**

699 Surface and bottom hydrography as well as the distribution of development stages for
700 individual years are available as online supplements (Figs S1-S4). Supplementary figures
701 presenting predicted versus observed values illustrate the information on predictive power of
702 individual covariates given in Table 4 (Figs S5-S8).

703

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989 **Table 1:** Survey cruises in this study. For the BONGO nets only the mesh size for the samples used in the analysis is given.

990

Year	Country	Survey ^a	Ship	Start Date	End Date	Gear	Mesh size (µm)	Nos. Hauls
2004	NL	PLACES	Tridens II	1.3.04	4.3.04	Gulf VII	270	64
	DE	PLACES	Heinke	16.2.04	23.2.04	BONGO	500	51
	UK	PLACES	Corystes	18.2.04	8.3.04	Gulf VII	270	137
	DK	PLACES	Dana	25.2.04	6.3.04	BONGO	330	100
	NO	PLACES	Haakon Mosby	8.3.04	23.3.04	Gulf III	330	86
2009	SC	PGEGGS	Scotia	20.2.09	6.3.09	BONGO	350	53
	FR	add. IBTS	Thalassa	17.1.09	13.2.09	WP2	500	136
	NO	add. IBTS	G. O. Sars	8.2.09	21.2.09	Gulf VII	280	57
	NL	IHLS	Tridens II	19.1.09	22.1.09	Gulf VII	280	69
	DK	add. IBTS	Dana	31.1.09	17.2.09	BONGO	330	68

991

992 ^a) **Abbreviations:** add. IBTS = Additional IBTS-Sampling, IHLS = International Herring Larvae Surveys, PLACES = Plaice and Cod Egg

993 Surveys, PCEGGS = Planning Group on North Sea Cod and Plaice Egg Surveys

994 **Table 2:** Syrjala-test between Stage I and subsequent development stages, for each year and both years combined. P <0.5 indicates
 995 that the distribution patters are significantly dissimilar.
 996

	Stage II				Stage III				Stage IV				Stage V			
	Cramér–von		Kolmogorov		Cramér–von		Kolmogorov		Cramér–von		Kolmogorov		Cramér–von		Kolmogorov	
	Mises		- Smirnov		Mises		- Smirnov		Mises		- Smirnov		Mises		- Smirnov	
	Ψ	p	Ψ	p	Ψ	p	Ψ	p	Ψ	p	Ψ	p	Ψ	p	Ψ	p
2004																
Cod	1.58	0.072	0.18	0.067	0.70	0.546	0.13	0.532	3.92	0.181	0.28	0.139	4.40	0.114	0.29	0.032
Haddock	2.85	0.004	0.22	0.018	1.36	0.061	0.16	0.098	3.78	0.004	0.26	0.012	4.91	0.003	0.33	0.001
Whiting	4.14	0.014	0.22	0.038	2.21	0.221	0.23	0.491	7.27	0.073	0.28	0.274	22.5	0.032	0.47	0.024
Plaice	0.44	0.254	0.11	0.362	1.01	0.061	0.12	0.345	3.39	0.001	0.26	0.002	4.67	0.001	0.31	0.002
2009																
Cod	5.62	0.097	0.33	0.073	5.42	0.062	0.35	0.062	7.09	0.016	0.38	0.011	5.12	0.076	0.35	0.049
Haddock	1.25	0.170	0.27	0.179	1.02	0.202	0.27	0.091	0.67	0.309	0.17	0.488	2.04	0.107	0.33	0.115
Whiting	0.84	0.018	0.25	0.203	0.67	0.075	0.25	0.133	1.59	0.06	0.36	0.305	2.52	0.112	0.54	0.101

[illegible]

Table 3: Model formulae, explained deviation, AIC, BIC and Moran's I in the residuals for the best fitting GAMMs fit to presence/absence and density of fish eggs. Of the Moran's I only the values for the first lag are presented.

Species	Type	N	Model Formula ^a	GAM - Dev. Expl. (%)	AIC	BIC	Moran's I ^b
Cod	Presence/absence	696	YD + s(b_depth, 4) + s5, (1 MEV2) + (1 MEV5)	18.5	688.1	720	0.04**
	Egg density	510	s(YD, 4) + s(b_depth, 4) + s(t5, 4), (1 MEV2) + (1 MEV5)	14.6	1131.2	1173.6	0.23**
Haddock	Presence/absence	696	s(YD, 4) + s(b_depth, 4) + s(tb, 4) + cs.(sb) + σ_{tgb} , (1 MEV3) + (1 MEV10) + (1 MEV28) + (1 MEV83)	57.3	478.5	537.6	0.07**
	Egg density	336	YD + s(b_depth, 3) + s(tb, 3) + s(sb, 3) + σ_{tgb} , (1 MEV3) + (1 MEV10) + (1 MEV28) + (1 MEV83)	42.6	725.3	778.7	0.05**
Whiting	Presence/absence	696	s(YD, 4) + b_depth + tb + s(σ_{tgb} , 4), (1 MEV2)	29.8	672.8	709.2	0.02*
	Egg density	448	s(YD, 4) + s(b_depth, 4) + s(t5, 4) + s(s5, 4) + σ_{tg5} , (1 MEV2)	34.8	1081.8	1131.0	0.12**
Plaice	Presence/absence	696	s(YD, 4) + s(b_depth, 4) + tb, (1 MEV2) + (1 MEV8) + (1 MEV12) + (1 MEV15)	21.4	808	853.5	0.02**
	Egg density	363	s(YD, 4) + s(b_depth, 4) + s(t5, 4) + s(s5, 4) + σ_{tg5} , (1 MEV2) + (1 MEV8) + (1 MEV12) + (1 MEV15)	29.3	655.1	713.5	0.18**

1002 ^a) Model formulae show the fixed-effects covariates, either as linear or smooth (s()) terms with degrees of freedom. The prefix cs. indicates
1003 a scaling function applied to a linear term. Explained devation was calculated with a GAM using the same fixed effects. MEVs were
1004 included as random covariates, e.g. (1|MEV1). YD, day of the year; b_depth, bottom depth; t5, temperature at 5 m depth; s5, salinity at 5 m
1005 depth; σ_t5 , gradient of σ_t at 5 depth; tb, bottom temperature; sb, bottom salinity; σ_tgb , gradient of σ_t at the bottom. MEVs
1006 ^b) Significance levels: **: ≤ 0.001 , *: > 0.001

Table 4: Predictive performance of the selected models and single covariates. The performance for presence/absence models is given as Receiver Operating Characteristic Area Under the Curve (ROC AUC) while for the egg densities it is the r^2 between predictions and observations. N is 636 for presence/absence of all species, for the non-zero abundance it is: $N_{\text{Cod}}=510$, $N_{\text{Haddock}}=336$, $N_{\text{Whiting}}=448$, $N_{\text{Plaice}}=363$.

Response	Covariates ^a	Cod	Haddock	Whiting	Plaice
Presence/Absence (ROC AUC)	Selected Model	0.71	0.85	0.79	0.74
	Year Day	0.64	0.78	0.72	0.63
	Bottom Depth	0.54	0.77	0.50	0.71
	Temperature5	-	-	-	-
	Salinity5	0.50	-	-	-
	σ_t -Gradient5	-	-	-	-
	Temperatureb	-	0.77	0.60	0.63
	Salinityb	-	0.81		-
	σ_t -Gradientb	-	0.63	0.62	-
	Random	0.50	0.50	0.50	0.50
Egg Density (r^2)	Selected Model	0.45	0.62	0.72	0.51
	Year Day	0.38	0.38	0.59	0.35
	Bottom Depth	0.42	0.56	0.61	0.39
	Temperature5	0.42	-	0.57	0.43
	Salinity5	-	-	0.58	0.38

σ_t -Gradient5	-	-	0.59	0.31
Temperatureb	-	0.50	-	-
Salinityb	-	0.53	-	-
σ_t -Gradientb	-	0.35	-	-
Random	0.36	0.34	0.56	0.30

1014

1015 ^{a)} Suffixes 5 and b indicate whether a value was measured at the surface (5 m) or at

1016 the bottom.

1017 **Table 5:** Log-likelihood ratio test between the selected models and models with
 1018 each of the covariates removed in turn. Bold font indicates significant p-values.

1019

Species	Dropped Covariate ^a	Presence/Absence			Egg density		
		$\chi^2_{0.05}$	df	p	$\chi^2_{0.05}$	df	p
Cod	Year Day	124.0	1	<0.001	2.2	1	0.13
	Bottom Depth	37.1	2	<0.001	10.2	1	0.001
	Temperature5	-	-	-	13.8	1	<0.001
	Salinity5	5.0	1	0.026	-	-	-
	σ_t -Gradient5	-	-	-	-	-	-
Haddock	Year Day	181.0	2	<0.001	4.8	1	0.029
	Bottom Depth	12.0	2	0.003	14.6	2	0.001
	Temperatureb	35.3	2	<0.001	0.9	2	0.622
	Salinityb	40.4	1	<0.001	15.9	2	<0.001
	σ_t -Gradientb	6.7	1	0.097	14.3	1	<0.001
Whiting	Year Day	134.9	2	<0.001	32.6	2	<0.001
	Bottom Depth	82.4	1	<0.001	79.6	2	<0.001
	Temperature5	-	-	-	24.1	2	<0.001
	Salinity5	-	-	-	0.8	2	0.658
	σ_t -Gradient5	-	-	-	5.4	1	0.020
	Temperatureb	34.1	1	<0.001	-	-	-
	Salinityb	-	-	-	-	-	-
	σ_t -Gradientb	2.0	2	0.374	-	-	-

Plaice	Year Day	35.5	2	<0.001	3.5	2	0.172
	Bottom Depth	78.2	2	<0.001	3.4	2	0.181
	Temperature5	-	-	-	19.1	2	<0.001
	Salinity5	-	-	-	1.8	2	0.408
	σ_t -Gradient5	-	-	-	0.6	1	0.426
	Temperatureb	9.5	1	0.002	-	-	-
	Salinityb	-	-	-	-	-	-
	σ_t -Gradientb	-	1	-	-	-	-

1020

1021 ^{a)} Suffixes 5 and b indicate whether a value was measured at the surface (5 m) or at

1022 the bottom.

Table 6: Variation explained by the fixed effects.

Covariates^a	Cod (%)	Haddock (%)	Whiting (%)	Plaice (%)
Presence/Absence				
Year Day	16.1	33.2	25.7	1.3
Bottom Depth	3.1	27.2	10.8	8.6
Temperature	-	33.0	15.3	8.3
Salinity and σ_{tg}	0.9	22.0	5.1	-
Total	15.9	47.1	29.1	9.6
Egg density				
Year Day	1.7	7.0	1.7	4.4
Bottom Depth	2.1	17.4	4.5	2.9
Temperature	5.0	21.4	6.8	1.1
Salinity and σ_{tg}	-	28.9	9.2	7.9
Total	5.0	30.5	9.9	13.2

^a) Variation partitioning only allows for four components. Therefore salinity and density gradient were, if necessary, grouped. Values for single covariates contain a pure component and a component shared with other covariates. Hence, the terms sum up higher than the total variation explained. σ_{tg} = density gradient

1030 **Table 7:** Log-likelihood ration test between GAMM and corresponding GAM models for
1031 presence/absence as well as density of eggs for the four species.

Species	Type	AIC		BIC		Log-likelihood ratio test		
		GAMM	GAM	GAMM	GAM	$\chi^2_{0.05}$	df	p
Cod	Presence/Absence	1938.8	1930.0	1957.0	1939.1	4.8	2	0.09
	Egg density	1079.6	1076.2	1096.6	1084.7	0.6	2	0.75
Haddock	Presence/Absence	1626.6	1613.4	1653.9	1622.5	5.2	4	0.26
	Egg density	672.5	659.7	695.4	667.3	4.8	4	0.31
Whiting	Presence/Absence	1921.2	1914.4	1934.8	1923.5	4.7	1	0.03
	Egg density	1005.6	998.7	1017.9	1006.9	4.9	1	0.03
Plaice	Presence/Absence	2046.1	2037.9	2073.3	2046.9	0.2	4	1.0
	Egg density	584.8	574.2	608.1	582.0	2.6	4	0.6

1032

Figure 1: Panel (a) shows the ichthyoplankton stations for 2004 and 2009 over a bathymetric map of the North Sea. Panel (b) exhibits the operational installations related to oil extraction; color-coded depending on the operating country on the same bathymetric map. Red lines depict Exclusive Economic Zones (EEZs). Areas shaded pink; show the areas with planned or ongoing seismic surveys in the Norwegian and Dutch sectors. Germany is not conducting seismic surveys and for the UK and Denmark no information is publicly available.

Figure 2: Mean Temperature and Salinity at the surface (5 m; panels (a, b) and at bottom depth (c, d), based on data from the first quarter of 2004 and 2009. Black dots indicate individual CTD hauls.

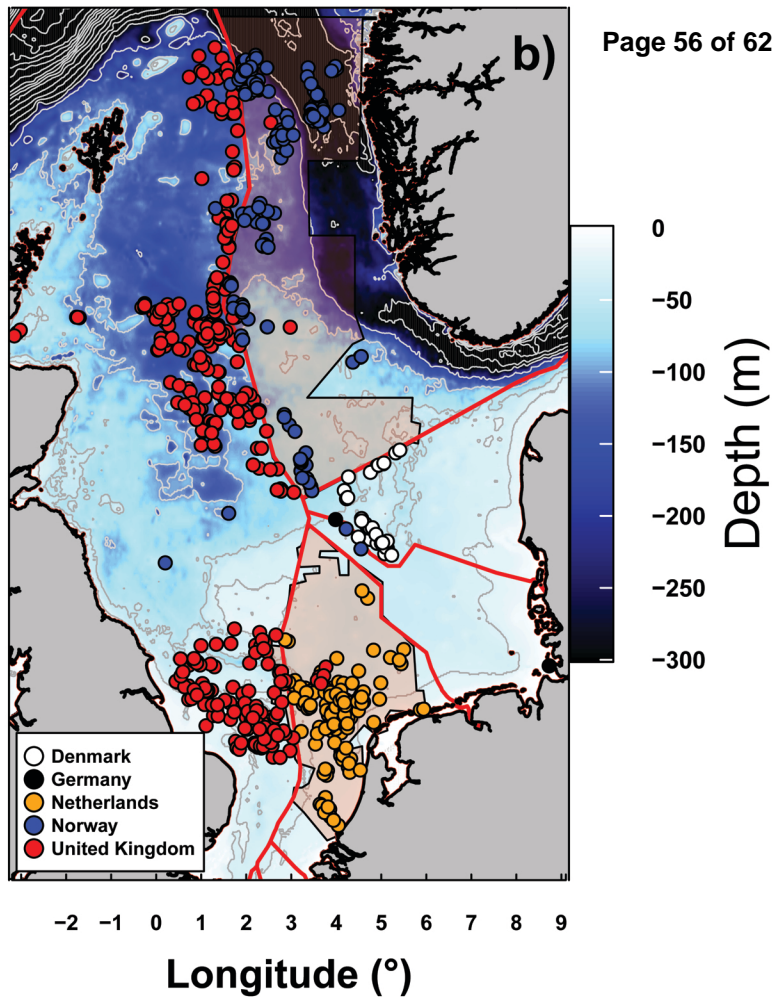
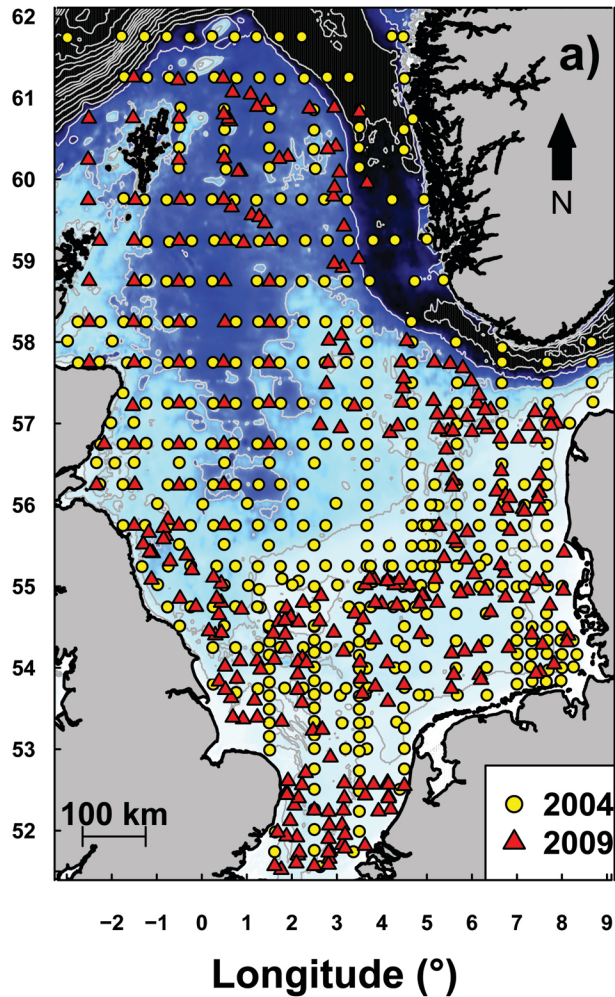
Figure 3: Range of structures of spatial autocorrelation (a) for the individual species. Broken lines indicate where the structures were grouped into the scales depicted, in the order fine to broad, on the maps on panels (b) to (e). The plotted structures are those for haddock, except on medium-broad scale (d) where there was only a single structure, for cod.

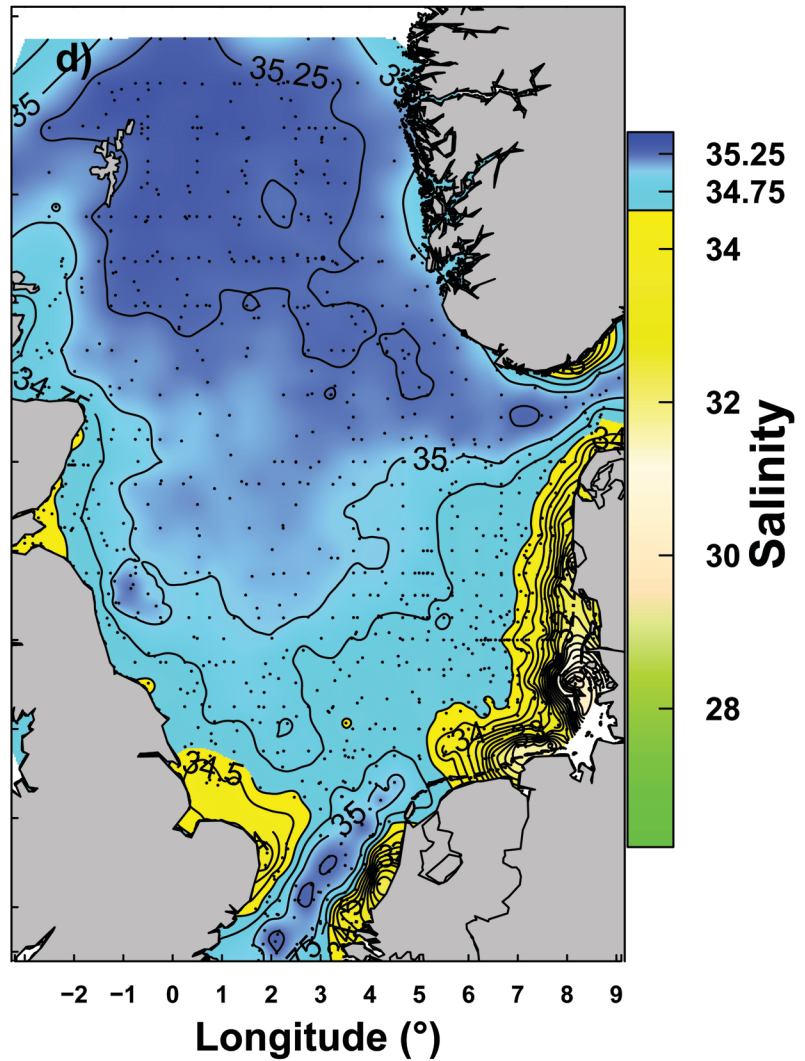
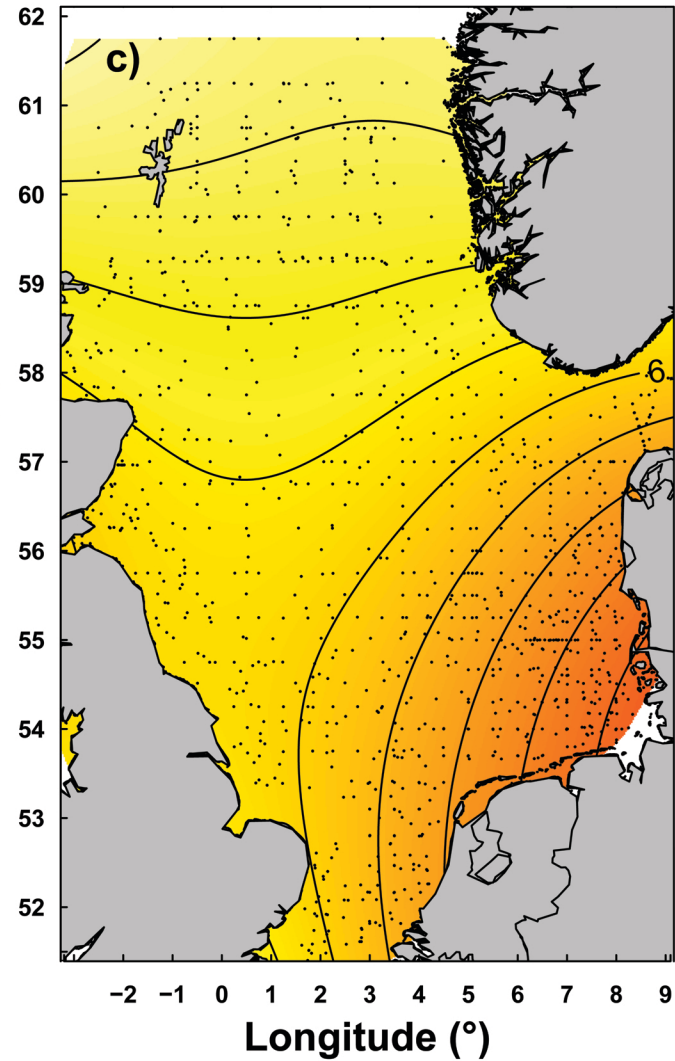
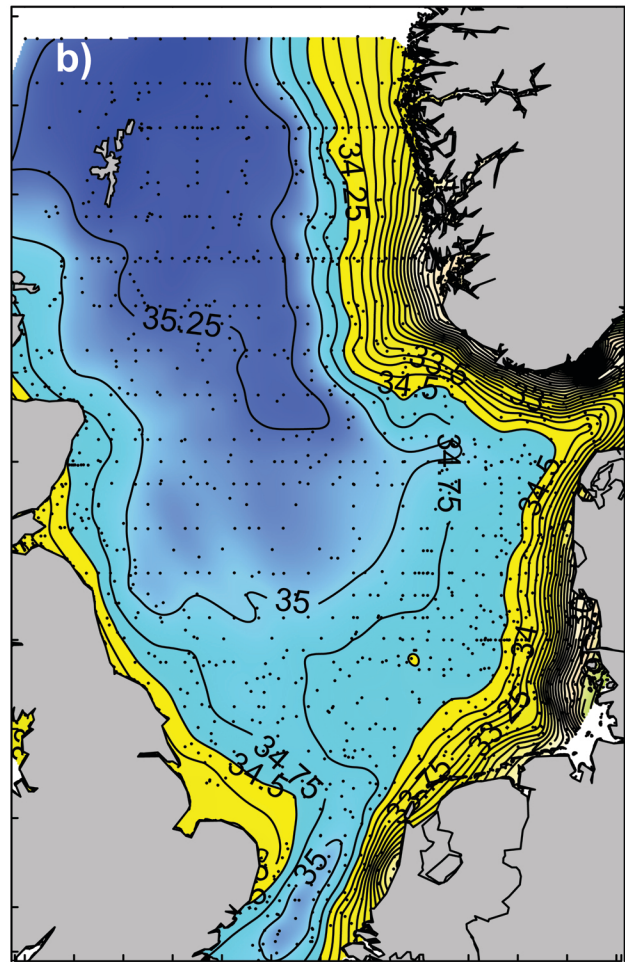
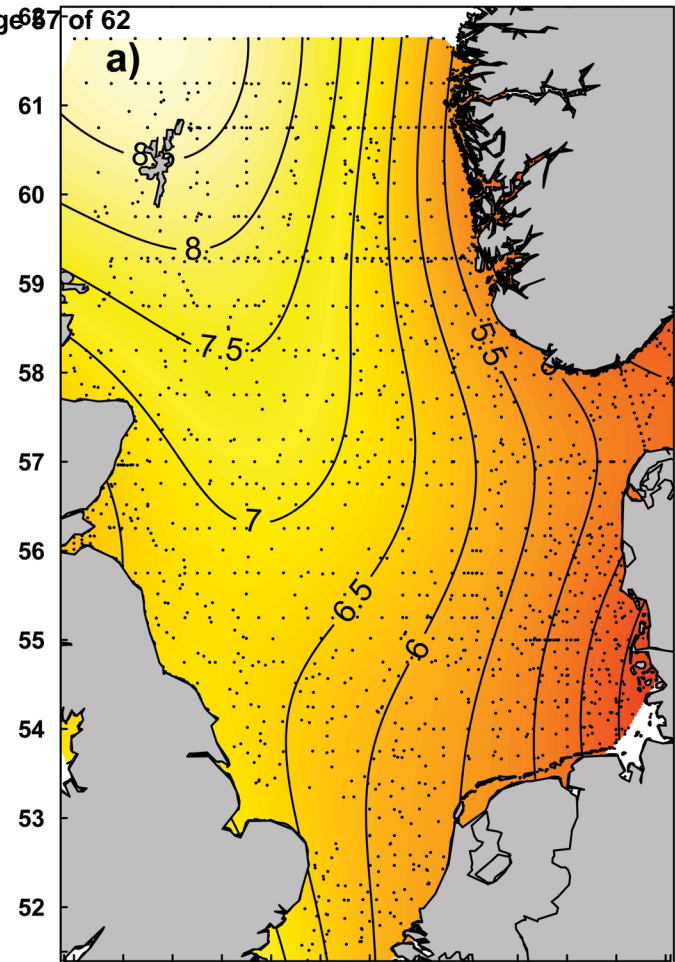
Figure 4: Mean interpolated surfaces for the distribution of eggs in each stage, drawing from both surveys. Interpolated areas beyond 200 m bottom depth are blanked out. Black dots on panel (a) indicate the sampling stations for both years.

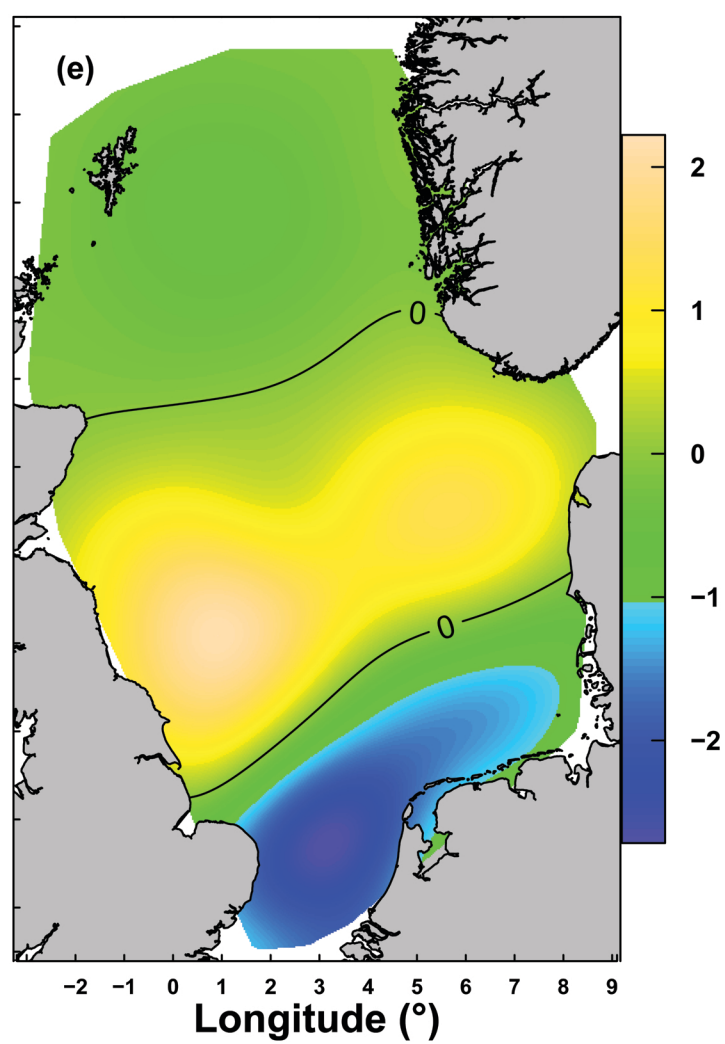
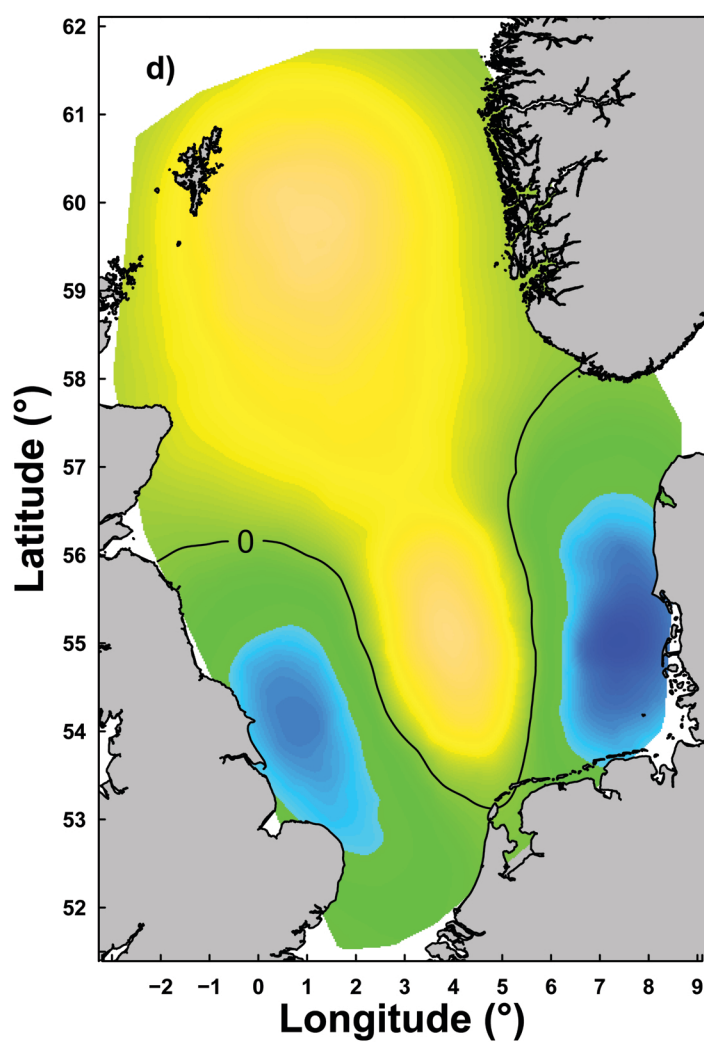
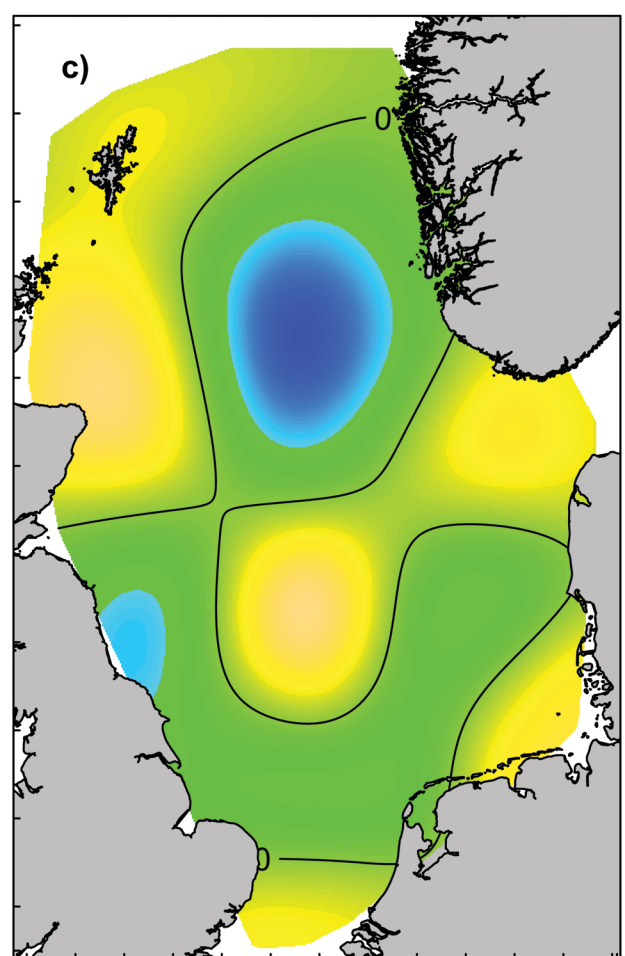
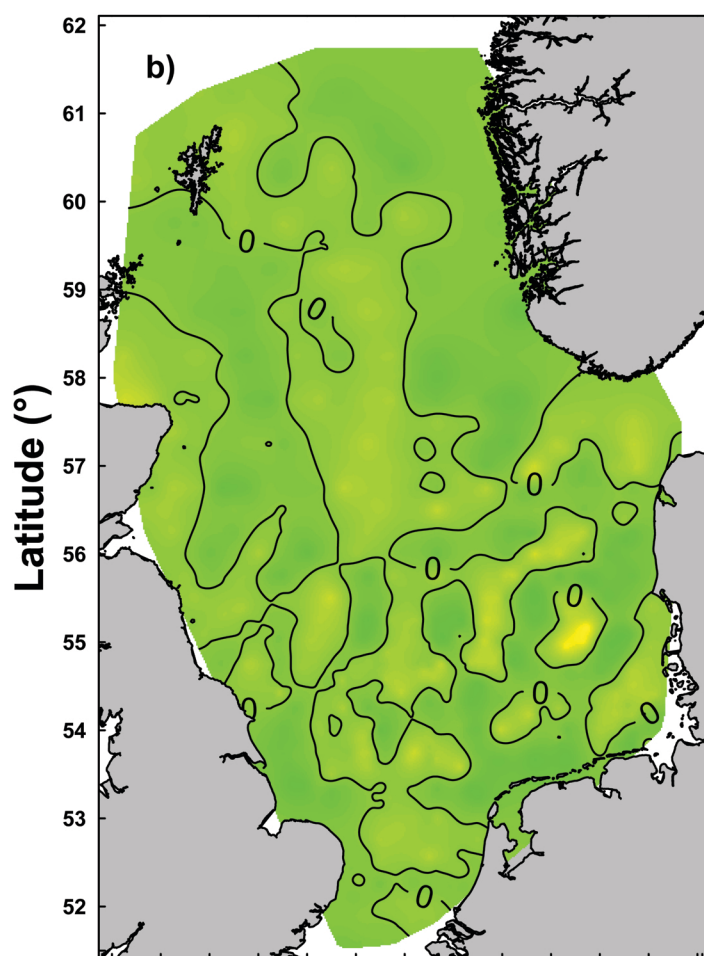
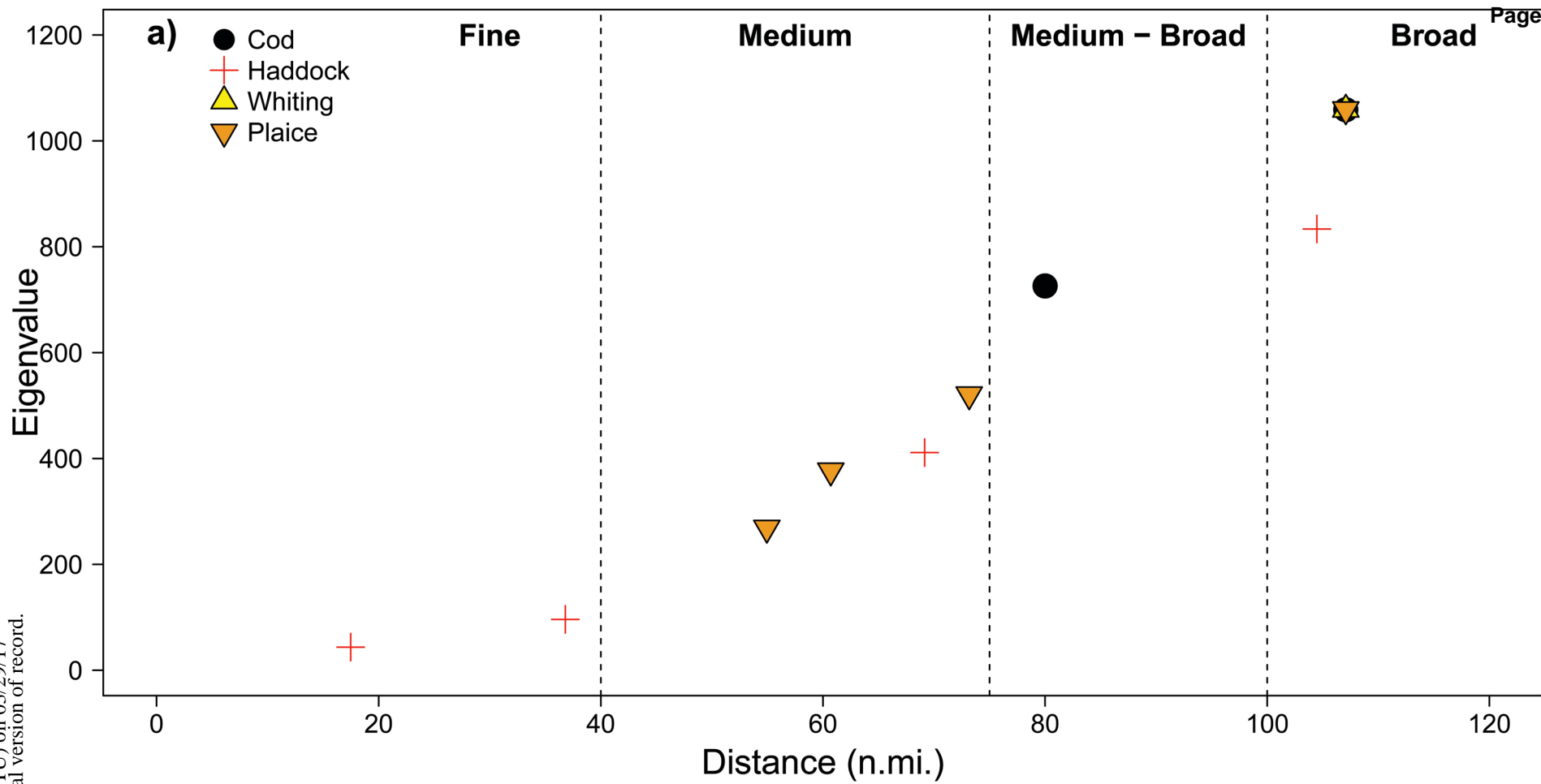
Figure 5: Predicted probability of occurrence for stage I eggs of all four species, on the range of the covariates in the best fitting models. Broken lines indicate models using hydrographic values measured at the surface. Hatches at the bottom of each panel indicate the values observed at samples. As cod was related to surface salinity, while haddock was related to bottom salinity on a narrower range, the corresponding observations are depicted in colours corresponding to the smooth terms. Shaded areas indicate the 95% confidence interval.

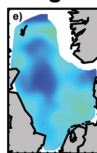
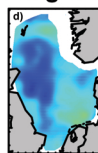
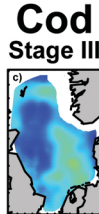
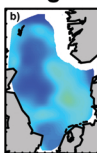
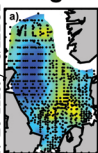
Figure 6: Predicted log-transformed stage I egg density for stage I eggs of all four species, related to the covariates in the best fitting models. Broken lines indicate models using hydrographic values measured at the surface. Observations with non-zero egg densities for the individual species are indicated by hatches, in the same colour as the smooth term, at the bottom of each panel. Shaded areas indicate the 95% confidence interval.

Figure 7: Panel (a) shows the average stage I egg density for each ICES rectangle on the interpolated surface of bottom temperature variability, based on CTD data for the 1st quarter of the entire 2000s. Panel (b) depicts installations of the oil industry, categorized as above-surface (red dots) or subsurface structures (white squares) the position of oil industry installation and the seismic survey areas for Norway and the Netherlands, shaded blue, on top of the average distribution of stage I eggs for all four species combined.

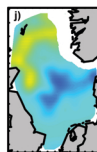
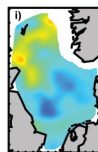
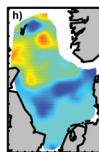
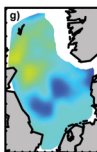
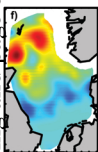




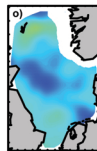
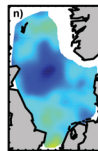
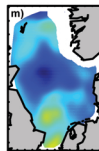
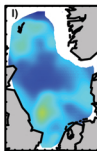
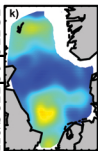




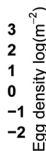
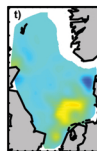
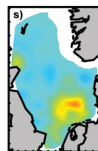
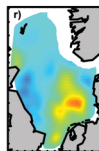
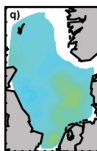
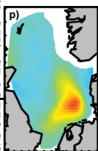
Haddock



Whiting



Plaice



Longitude (°)

Longitude (°)

Longitude (°)

Longitude (°)

Longitude (°)

